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TEMPORAL AND MATERNAL EFFECTS ON REPRODUCTIVE ECOLOGY OF THE GIANT GARTERSNAKE (*THAMNOPHIS GIGAS*)

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**ABSTRACT**—We used mixed-effects models to examine relationships of reproductive characteristics of the giant gartersnake (*Thamnophis gigas*) to improve population modeling and conservation planning for this species. Neonates from larger litters had lower mass, and mass of neonates also was affected by random variation among mothers. Length of mother did not affect relative mass of litters; however, our data suggest that longer mothers expended less reproductive effort per offspring than shorter mothers. We detected random variation in length of neonates among mothers, but these lengths were not related to length of mother or size of litter. Mean size of litter varied among years, but little evidence existed for a relationship between size of litter or mass of litter and length of mother. Sex ratios of neonates did not differ from 1:1.

**RESUMEN**—Se utilizaron modelos de efectos mixtos para examinar las relaciones de las características reproductivas de la serpiente (*Thamnophis gigas*) para mejorar el método para modelar poblaciones y la planificación de la conservación de esta especie. Camadas más grandes de recién nacidos tuvieron una menor masa, y la masa de recién nacidos también fue afectada por la variación aleatoria entre las madres. La longitud de la madre no afectó la masa relativa de la camada; sin embargo, nuestros datos sugieren que las madres más largas gastaron menos esfuerzo reproductivo por cría que madres más cortas. Detectamos variación aleatoria en la longitud de los recién nacidos entre madres, pero estas longitudes no fueron relacionadas ni con la longitud de la madre ni con el tamaño de la camada. El promedio del tamaño de la camada varió entre años, pero existió poca evidencia de una relación entre el tamaño o masa de la camada y la longitud de la madre. La proporción de los sexos en recién nacidos no difirieron de 1:1.

Because knowledge about reproductive ecology of organisms is essential for understanding their population ecology and evolution, it is one of the most-studied aspects of the biology of snakes (Seigel and Ford, 1987; Rossman et al., 1996). A few general trends have emerged across many species of snakes. For example, many species exhibit an increase in size of clutch (or litter) with length of mother (Seigel and Ford, 1987). Viviparous species have lower relative mass of litter (ratio of total mass of litter to mass of mother after parturition) than oviparous species (Seigel and Fitch, 1984). The lower reproductive effort of viviparous species might be associated with reduced locomotor ability of gravid females, which places an additional cost of reproduction on viviparous snakes (Seigel et al., 1987). Despite these broad generalizations, little is known about reproductive ecology of many

species of snakes, particularly those that are secretive, tropical, or rare. This dearth of knowledge about reproductive ecology of rare snakes is particularly unfortunate because of the importance of reproduction to viability of populations (Shine and Bonnet, 2009).

Because of its limited distribution, rarity, cryptic coloration, and secretive behavior, relatively little is known about the reproductive ecology of the giant gartersnake (*Thamnophis gigas*). The giant gartersnake is the largest and most aquatic of the gartersnakes, and like other gartersnakes, it is viviparous (Rossman et al., 1996). The giant gartersnake is endemic to wetlands in the Central Valley of California (Fitch, 1940; Hansen and Brode, 1980). Because of extensive loss of its wetland habitat (Frayer et al., 1989), the species is listed as threatened at both the state and federal levels (California

TABLE 1—Reproductive characteristics of the giant gartersnake (*Thamnophis gigas*). Where appropriate, means and confidence intervals (*CI*) were calculated from the null (intercept-only) linear mixed model for each parameter to account for non-independence of observations from the same litter.

Reproductive characteristic	<i>n</i>	Mean	95% <i>CI</i> <sup>a</sup>
Snout–vent length of mother (mm)	11	815	692–974
Mass of mother, pre-parturition (g)	6	377	257–585
Mass of mother, post-parturition (g)	6	267	205–453
Date of parturition	11	13 August	11 July–4 October
Size of litter	11	17	13–21
Mass of litter (g)	11	68.38	55.57–81.19
Snout–vent length of neonate (mm)	168	208.8	196.5–221.1
Mass of neonate	168	4.87	4.07–5.67
Relative mass of litter	6	0.26	0.22–0.30
Relative mass of litter per offspring	6	0.019	0.017–0.021

<sup>a</sup> For snout–vent length of mother; mass of mother, pre-parturition; mass of mother, post-parturition; and date of parturition, the 95% *CI* is replaced by the range.

Department of Fish and Game Commission, 1971; United States Fish and Wildlife Service, 1993). To assist in planning its recovery and modeling populations, we used mixed-effects models to examine relationships in size and mass of litters, length and mass of neonates, and reproductive effort in relation to length of mother, year, and random effects of mother.

**MATERIALS AND METHODS**—We collected 11 gravid females from four sites (Badger Creek, 38.32°N, 121.33°W, 7 m elevation, *n* = 2; Colusa National Wildlife Refuge, 39.15°N, 122.04°W, 13 m, *n* = 1; Gilsizer Slough, 39.00°N, 121.71°W, 8 m elevation, *n* = 6; and Sacramento National Wildlife Refuge, 39.41°N, 122.16°W, 24 m elevation, *n* = 2) in the Central Valley of California during June and early July 1995 (*n* = 4), 1996 (*n* = 2), and 1997 (*n* = 5). These individuals had been implanted previously with radiotransmitters and were recaptured during the parturition period to replace radiotransmitters or to repair superficial wounds related to abrasion from subcutaneous antennas. Each snake was housed individually in a glass terrarium, provided water ad libitum, and offered food (small fish or tadpoles) daily. Gravid females rarely ingested prey, so no effect of providing food to females on mass of post-parturition females was observed. We observed individuals daily to determine date of parturition. Within 24 h of parturition, we recorded size and mass (g) of litter, and snout–vent length (mm), total length (mm), mass (g), and sex of each neonate. In 1996 and 1997 (*n* = 6), we weighed mothers to determine mass at pre-parturition and post-parturition (g); mass at pre-parturition was obtained 9–37 days prior to parturition and mass at post-parturition was obtained when measurements of neonates were taken. We measured relative mass of litter as total mass of litter divided by mass of mother after parturition. We quantified allocation of reproductive effort to individual offspring of each female by dividing relative mass of litter by size of litter (hereafter

referred to as relative mass of litter per offspring; Ford and Killebrew, 1983). Following measurements in the laboratory, we released neonates and mother at the site of capture of the mother.

We examined variation in reproductive parameters by comparing linear models using information criteria (Anderson, 2008). We examined effects of snout–vent length of mother and year on size and total mass of litter, relative mass of litter, and relative mass of litter per offspring. We used linear mixed models with mother as a random effect to examine effects of size of litter and snout–vent length of mother on snout–vent length and mass of neonate. We did not test for effects of site because of small samples (Bolker et al., 2009). We used logistic regression to examine effect of snout–vent length of mother on presence of dead material (stillborns or unfertilized yolks) in the litter (Sparkman et al., 2007). In all cases, we compared models using Akaike’s Information Criterion corrected for small samples (AIC<sub>c</sub>; Burnham and Anderson, 2002). We also used a test of given proportions to examine if sex ratio of litters differed from each other and from a sex ratio of neonates of one, and an exact binomial test to examine if overall sex ratio of neonates was one. We used program R 2.7.2 (R Development Core Team, 2008) for all analyses, and lme4 (D. Bates et al., <http://lme4.r-forge.r-project.org/>) for analysis of mixed models.

**RESULTS**—Gravid females in our study typically lost ca. 100 g upon parturition (Table 1). Size of litter varied among years (Table 2), but total mass of litter was not affected by size of mother or year (Table 2). Although relative mass of litter was not affected by snout–vent length of mother, longer females expended less reproductive effort per offspring than shorter females ( $-2.6 \times 10^{-5}$  relative mass of litter per offspring units per mm of snout–vent length of mother; 95% *CI* =  $-4.0 \times 10^{-5}$  to  $-1.2 \times 10^{-5}$ ; Fig. 1). Random effects

TABLE 2—Results of model-fitting procedures for reproductive characteristics of the giant gartersnake (*Thamnophis gigas*). Within each reproductive characteristic, models are listed in order of decreasing support. All models include an intercept; models noted as constant include only an intercept. Random effects are indicated by variables in parenthesis.

Reproductive characteristic and model	Log-likelihood	Number of parameters	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Weight
Size of litter					
Year	−27.40	3	64.21	0	0.85
Constant	−33.06	1	68.57	4.36	0.10
Snout–vent length of mother	−32.04	2	69.59	5.38	0.06
Mass of litter					
Constant	−49.45	1	101.34	0	0.70
Snout–vent length of mother	−48.86	2	103.22	1.89	0.27
Year	−49.36	3	108.15	6.81	0.02
Snout–vent length of neonate					
Constant + (mother)	−591.4	2	1,186.87	0	0.88
Size of litter + (mother)	−592.7	3	1,191.55	4.67	0.09
Snout–vent length of mother + (mother)	−593.7	3	1,193.55	6.67	0.03
Mass of neonate					
Size of litter + (mother)	−118.5	3	243.15	0	0.48
Constant + (mother)	−120.0	2	244.07	0.93	0.30
Snout–vent length of mother + (mother)	−119.3	3	244.75	1.60	0.22
Relative mass of litter					
Constant	9.35	1	−15.70	0	0.88
Snout–vent length of mother	9.85	2	−11.71	3.99	0.12
Year	10.48	3	−2.96	12.75	<0.01
Relative mass of litter per offspring					
Snout–vent length of mother	31.00	2	−54.00	0	0.88
Constant	26.54	1	−50.08	3.92	0.12
Year	36.54	3	−35.09	18.91	<0.01
Presence of dead material in litter					
Snout–vent length of mother	−5.88	2	17.26	0	0.44
Constant	−7.58	1	17.60	0.35	0.37
Year	−4.75	3	18.93	1.68	0.19

of mother were stronger than snout–vent length of mother or size of litter for predicting snout–vent length of offspring (effects of mother,  $SD = 15.44$ , residual  $SD = 7.25$ ; Fig. 2). A random effect of the mother on mass of neonates also existed (effects of mother,  $SD = 0.57$ , residual  $SD = 0.44$ ), but little evidence existed for an effect of size of litter on mass of neonates (evidence ratio = 1.59; Table 2). Evidence for a relationship between length of mother and presence of dead material in the litter was weak (evidence ratio = 1.19; Table 2). Sex ratios of neonates within litters was 0.67–2.00, but sex ratios did not differ among litters ( $\chi^2 = 3.33$ ,  $df = 9$ ,  $P = 0.950$ ) or from one ( $\chi^2 = 3.44$ ,  $df = 10$ ,  $P =$

0.969). Overall sex ratio of neonates in our study was 0.95, which also did not differ from one (95%  $CI = 0.67$ – $1.33$ ).

DISCUSSION—Our study provided important information regarding biology, conservation, and management of giant gartersnakes. Longer females expended less reproductive effort per offspring than shorter females, but total reproductive effort did not vary with length of female. This pattern also has been observed in other viviparous natricine snakes (Ford and Killebrew, 1983; King, 1993), suggesting that longer females in this group allocate reproductive effort to more, rather than larger, offspring (King, 1993).

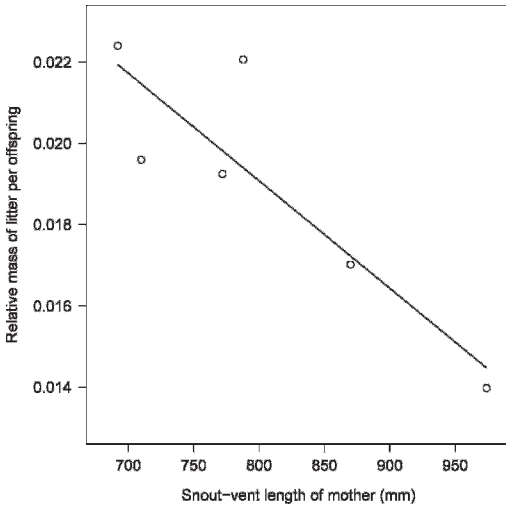


FIG. 1—Relationship of snout-vent length of mother to relative mass of litter per offspring of the giant gartersnake (*Thamnophis gigas*).

Size of offspring might be relatively fixed within species of viviparous natricine snakes, so that the only option available for larger females to increase reproductive output is to produce additional offspring. The positive relationship between size of litter and availability of energy, and concomitant lack of a relationship between availability of energy and size of neonate (Ford and Seigel, 1989), supports existence of constraints on size of neonates.

Evidence for a random effect of mother on size of neonate (length and mass), rather than a relationship between size of neonate and snout-vent length of mother, further supports the hypothesis that size of mother is not related to size of offspring in the giant gartersnake. The source of variation among mothers in size of neonates currently is unknown, but could be the result of several mechanisms. Genetic differences are, perhaps, the most obvious potential source of among-female variability in size of offspring (Ford and Seigel, 1989). It also is possible that differences in success of foraging among females might contribute to differences in size of neonates. This explanation is unlikely because dietary differences in captive snakes did not reveal an effect on length or mass of neonates (Ford and Seigel, 1989). Trade-offs between number and size of offspring are common elements of life-history theory (King, 1993), and our data suggested a weak, negative effect

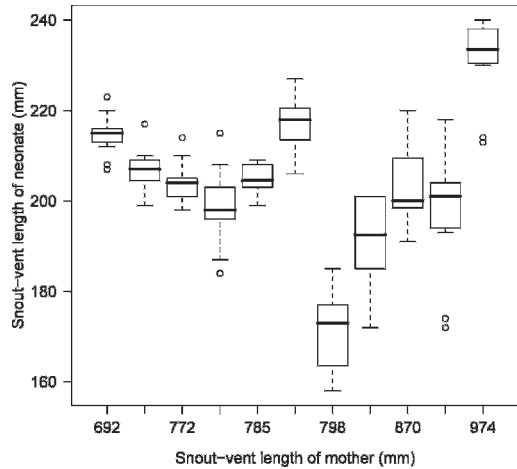


FIG. 2—Snout-vent lengths of neonates for litters of giant gartersnakes (*Thamnophis gigas*), indicating the strong random effect of the mother. The X-axis is not to scale but displays values of snout-vent length of mothers for each litter in ascending order.

of size of litter on mass of neonates. However, no such relationship existed between size of litter and snout-vent length of neonates. Identifying the source of among-litter variation in size of neonates, and determining if differences in size result in differences in survival of juveniles, are areas for future research that could have direct conservation and management implications.

Our data also suggest that, like many other species of snakes, size of litters of giant gartersnakes vary among years (Seigel and Fitch, 1985). These temporal effects on size of litter were stronger than effects of size of mother, which were reported as important elsewhere (Seigel and Ford, 1987). Temporal variation in reproductive output might be related to variation in quantity or quality of prey among years (Ford and Seigel, 1989; Winne et al, 2006). Another potential mechanism that could account for annual variation in size of litters is residual effects of reproduction in prior years (Lourdais et al., 2002). Many studies have reported that larger females produce larger clutches or litters (Seigel and Ford, 1987). An effect of size of mother on size of litter could be masked, however, if females reproduce in years when they do not have enough energy to maximize reproductive effort (Shine, 2003). Nonetheless, identifying sources of temporal variation in size of litters might assist planning for recovery of the

giant gartersnake by minimizing conditions that lead to low reproductive output.

Because of its aquatic habits and relatively large size, the giant gartersnake might have different sizes of litters and reproductive effort compared to its congeners. Our estimate of mean size of litter was smaller, but mean snout-vent length of neonates was longer than previous estimates for the giant gartersnake (23 neonates/litter and 206 mm, respectively; Hansen and Hansen, 1990). Size of litters of the giant gartersnake was relatively large compared to other gartersnakes (range, 5.2–32.5 g; Rossman et al., 1996), but differences are difficult to interpret because of annual variation in size of litter (Seigel and Fitch, 1985; Ford and Seigel, 1989) and a general increase in size of litter with snout-vent length of mother (Ford and Killebrew, 1983; Seigel and Ford, 1987). Concomitantly, mean snout-vent length and mass of offspring were larger than nearly all other gartersnakes (range of mean snout-vent length of offspring, 99–217 mm; range of mean mass of offspring, 1.2–3.3 g; Rossman et al., 1996). Relative mass of litter was less for the giant gartersnake than for the Butler's gartersnake (*Thamnophis butleri*; mean = 0.562 g; Ford and Killebrew, 1983) and black-necked gartersnake (*Thamnophis cyrtopsis*; 0.614 g; Vitt, 1975), but similar to many other gartersnakes (range, 0.200–0.277 g; Seigel and Fitch, 1984; Larsen et al., 1993). Swimming ability is more strongly affected than terrestrial locomotion by presence of embryos (Shine, 1988). Therefore, it would be interesting to examine relationships between reproductive effort and position of the litter with degree of aquatic behavior among species of *Thamnophis*. Like the terrestrial gartersnake (*Thamnophis elegans*; Sparkman et al., 2007), longer (older) female giant gartersnakes were slightly more likely to have dead material in their litters.

Conservation of the giant gartersnake requires that, on average, reproduction offsets mortality within each generation. Identifying sources of temporal variation in litters might reveal potential management actions to improve reproductive output of populations. For example, managing habitat to increase abundance or availability of prey might allow females to produce larger litters that result in increased growth of populations (Shine and Bonnet, 2009). In addition to these temporal effects, studies of stage-specific

and sex-specific mortality are needed to assess impact of conservation practices on rates of growth of populations. Combined with data for stage-specific survival, our data for reproduction can be used to construct population models (Caswell, 2000) from which efficacy of different conservation strategies can be assessed.

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